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How deep is the conflict between molecular and fossil evidence on the age of angiosperms?

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Summary

The timing of the origin of angiosperms is a hotly debated topic in plant evolution. Molecular dating analyses that consistently retrieve pre-Cretaceous ages for crown-group angiosperms have eroded confidence in the fossil record, which indicates a radiation and possibly also origin in the Early Cretaceous. Here we evaluate paleobotanical evidence on the age of the angiosperms, showing how fossils provide crucial data for clarifying the situation. Pollen floras document a Northern Gondwanan appearance of monosulcate angiosperms in the Valanginian and subsequent poleward spread of monosulcates and tricolpate eudicots, accelerating in the Albian. The sequence of pollen types agrees with molecular phylogenetic inferences on the course of pollen evolution, but it conflicts strongly with Triassic and early Jurassic molecular ages, and the discrepancy is difficult to explain by geographic or taphonomic biases. Critical scrutiny shows that supposed pre-Cretaceous angiosperms either represent other plant groups or lack features that might confidently assign them to the angiosperms. However, the record may allow the late Jurassic existence of ecologically restricted angiosperms, like those seen in the basal ANITA grade. Finally, we examine recently recognized biases in molecular dating and argue that a thoughtful integration of fossil and molecular evidence could help resolve these conflicts.

Key words: angiosperms, paleobotany, palynology, molecular dating, Jurassic, Cretaceous

I. Introduction

The age of the angiosperms is a long-standing topic of debate. Beginning with Darwin, many botanists took the supposedly sudden appearance of diverse angiosperm leaves in the mid-Cretaceous as evidence that the group originated and radiated extensively before the Cretaceous in some area with no known fossil record. For example, Axelrod (1952, 1970) hypothesized that angiosperms originated in tropical uplands in the Permo-Triassic but only invaded lowland basins in the Cretaceous. In the 1960s, opinion began to shift toward the view that angiosperms originated not long before their Cretaceous appearance. Scott *et al.* (1960) and Hughes (1961) stressed the failure of palynologists to find angiosperm pollen in pre-Cretaceous rocks, despite nearly worldwide sampling, arguing that some pollen should have been transported into lowland basins even if angiosperms were restricted to the uplands. They also rejected reports of Triassic and Jurassic angiosperms that earlier authors had cited as support for a pre-Cretaceous origin. Others noted that the first Cretaceous angiosperm pollen was much less diverse than expected from earlier leaf identifications, and pollen morphological types appeared in an order corresponding to the course of pollen evolution inferred from comparative studies of extant plants (Doyle, 1969; Muller, 1970). Subsequent workers reinterpreted the record of angiosperm leaves (Hickey & Doyle, 1977) and flowers (Friis *et al.*, 2011) as showing a similar pattern of diversification. Some authors took these observations as evidence that angiosperms originated in the Cretaceous, but others cautioned that they might allow an earlier origin if pre-Cretaceous angiosperms were at a low level of morphological diversification (Doyle, 1969; Muller 1970).

By contrast, in the past three decades a great number of molecular dating analyses, based on the divergence of DNA sequences of living plants, have supported a pre-Cretaceous origin of crown-group angiosperms (see Box 1 for definitions) – sometimes Jurassic, but sometimes Triassic or even Permian (see Magallón *et al.*, 2015 and references therein). Late Jurassic ages might be consistent with the existence of low-diversity and ecologically restricted angiosperms (Feild *et al.*, 2004), but older dates are hard to reconcile with the congruence of the fossil record and neobotanical ideas on the evolution of pollen, leaves, and flowers, which have been independently confirmed by molecular phylogenetic analyses (Doyle, 2012). There have been new reports of pre-Cretaceous angiosperm fossils, but these have been questioned on various grounds (Doyle, 2012; Herendeen *et al.*, 2017).

Most molecular studies have not addressed these conflicts directly, but recently Barba-Montoya *et al.* (2018) argued that they reflect deep flaws in interpretation of the fossil record. In this review we summarize paleobotanical evidence on the early history of the angiosperms, organizing our discussion around the particularly extensive pollen record. We show that an informed reading of the fossil record may be consistent with a later Jurassic origin of crown-group angiosperms, but it militates against an older origin, and proposed direct fossil evidence for the existence of angiosperms in the Triassic and Jurassic is either erroneous, highly questionable, or inconclusive. We then discuss potential biases in molecular dating analyses that may have contributed to the conflict between fossil and molecular data and consider briefly the future role of fossil data.

II. Patterns in the Cretaceous record

In this survey, we concentrate on the pollen record, which is far better sampled spatially and temporally than the record of other plant parts. Before the Aptian (Fig. 1), practically the only convincing angiosperm megafossils are from the Barremian Las Hoyas flora of Spain (Gomez *et al.*, 2015) and the Yixian flora of northeastern China (Sun *et al.*, 2002, 2008), which straddles the Barremian-Aptian boundary (Chang *et al.*, 2017). Fossil flowers (usually mesofossils, in the millimeter size range, which often have pollen in stamens or on stigmas) are easier to associate with modern clades than pollen, but their record is still limited to relatively few formations, mostly Albian and younger in age. By contrast, there is an extensive pre-Aptian pollen record of angiosperms.

Some early workers took the first appearance of tricolpate pollen (now known back to the late Barremian) as the first definite record of angiosperms (e.g., Scott *et al.*, 1960; Brenner, 1963). Tricolpate pollen (Box 1) certainly represents evidence for crown-group angiosperms, since it is the most securely established morphological synapomorphy of the eudicot clade, which includes ca. 72% of living angiosperm species and is strongly supported as monophyletic by molecular data. Tricolpate pollen was modified within eudicots into derived types such as tricolporate (the most common type today) and triporate. However, many angiosperms have monosulcate pollen (Box 1), which has long been considered ancestral based on its association with other “primitive” features and its occurrence in gymnospermous seed plants (Wodehouse, 1936; Takhtajan, 1959). Significantly, palynological work in the 1960s showed that the first fossil tricolpates are preceded by monosulcate angiosperm pollen

(Doyle, 1969; Muller, 1970). Subsequently, the ancestral status of monosulcate pollen has been amply confirmed by molecular phylogenetics (Doyle, 2005). Eudicots are one of five clades making up the Mesangiospermae, which include 99.9% of angiosperm species, along with monocots, Magnoliidae, Chloranthaceae, and the aquatic genus *Ceratophyllum*. The remaining 0.01% constitute the basal "ANITA" lines, namely *Amborella*, Nymphaeales (water lilies), and Austrobaileyales. All of these groups except eudicots have monosulcate pollen or non-tricolpate pollen types thought to be derived from monosulcate (e.g., disulculate, zonasulculate, inaperturate: Box 1).

The concept of tricolpates as the first definite evidence of crown angiosperms was reaffirmed by Barba-Montoya *et al.* (2018), who took the well-nested position of eudicots as support for a long prior history of angiosperms. They recognized the existence of an earlier monosulcate phase but considered it phylogenetically ambiguous. However, this phase is actually quite extensive and informative. In the following sections we survey the monosulcate and subsequent phases and their phylogenetic implications. For a quantitative assessment of the congruence of the pollen record with molecular dating studies, we complement this survey with an analysis of the diversity of major pollen types through time predicted by a dated molecular tree.

Temporal and spatial patterns in the pollen record. The first indication of a monosulcate phase in the angiosperm record was the description by Couper (1958) of *Clavatipollenites* from the Barremian (upper Wealden) of England. This fossil differs from the monosulcate pollen of gymnosperms in having columellar exine structure, with radial rods connecting the inner (nexine) and outer (tectum) layers (Doyle *et al.*, 1975; Fig. 1). Later SEM studies (Hughes *et al.*, 1979) showed that Couper's (1958) material consisted of several types that differ in microsculpture, but they are all columellar and reticulate, with the tectum consisting of bridges (muri) linking the heads of the columellae to form a network. Many authors have used the name *Clavatipollenites* for finely reticulate pollen with spinules on the muri and a sculptured sulcus. TEM studies (Doyle *et al.*, 1975; Walker & Walker, 1984) showed that Aptian pollen of this type from the Potomac Group of the eastern USA is also angiosperm-like in lacking the laminated, distinctly staining inner nexine layer (endexine) all around the grain in gymnosperms. Instead, endexine is restricted to the sulcus, and the rest of the nexine consists of ectexine (foot layer), like the columellae and tectum.

Intensive SEM studies on the Wealden (Hughes *et al.*, 1979; Hughes & McDougall, 1990; Hughes, 1994) showed low-frequency but diverse angiospermous monosulcates extending back to the Hauterivian, which vary in coarseness of the reticulum and microsculpture of the muri. A divergent element is *Tucanopollis* ("Barremian-*ring*" of Hughes, 1994), first described from the Barremian and Aptian of Brazil (Regali *et al.*, 1974; Regali, 1989), which has a continuous rather than a reticulate tectum but internal exine structure and sulcus sculpture like *Clavatipollenites* (Doyle & Hotton, 1991).

In the 1970s, it became clear that some aspects of the pollen record in other geographic areas differed from what is seen in England and the eastern USA. These differences indicate that there are migrational as well as evolutionary patterns in the record, but they do not contradict the general evolutionary scheme. The British and Potomac floras represent Brenner's (1976) Southern Laurasia province, which extends east to Kazakhstan and China. The data support a modified version of the poleward migration theory of Axelrod (1959), originally based on leaf floras. The picture is summarized in Fig. 2, with four paleogeographic maps showing important pollen sequences, selected because they are particularly well studied and well dated by marine fossils or by palynological correlations with marine sediments in the same province, and Fig. 3, with first occurrences in these sequences of monosulcate and tricolpate angiosperm pollen, plotted against paleolatitude and time. These sequences are only a fraction of those that are known, but most others are less intensively studied, less confidently dated, and/or cover only short stratigraphic intervals. Many of the publications involved are several decades old, but the picture is corroborated by more recent studies in both previously and newly investigated areas.

An important advance was recognition that tricolpate pollen (initially with reticulate sculpture) appears consistently earlier in Brenner's (1976) Northern Gondwana province, including the late Barremian and Aptian of Brazil (Brenner, 1976; Regali & Viana, 1989), Gabon (pollen Zone C-VII; Doyle *et al.*, 1977), and Israel (Brenner, 1976, 1996). Some occurrences originally considered Aptian are now thought to be late Barremian, based in part on association with the distinctive pollen genus *Afropollis*, which appears in the dated late Barremian of several areas (Doyle *et al.*, 1982; Hughes & McDougall, 1990; Doyle, 1992). Non-angiospermous dominants indicate arid tropical climates in some parts of this province (*Classopollis*, ephedroid pollen) and wetter conditions (more fern spores) in others (Brenner, 1976, 1996; Doyle *et al.*, 1982; Mejia-Velasquez *et al.*, 2018).

Significantly, however, Zone C-VII and older sediments in Gabon and Congo (Zones C-V and C-VI: Doyle *et al.*, 1977; Doyle, 1992) and Brazil (Regali & Viana, 1989) contain many of the same monosulcate angiosperm types seen in the Wealden, including reticulate monosulcates and especially abundant *Tucanopollis*. Later, in Zones C-VIII and C-IX (Aptian), angiosperms are more diverse, including tricolpates with striate as well as reticulate sculpture. Consistent pollen sequences have been described from Egypt (Schrank, 1983, 1992; Penny, 1991; Ibrahim, 2002; Schrank & Mahmoud, 2002) and Israel (Brenner, 1996). Reticulate monosulcate pollen is known from the Valanginian of Israel (Brenner, 1996) and Italy (Trevisan, 1988), which was located at the northern edge of Gondwana.

In Asian paleoequatorial areas, pre-Albian floras are like those of Northern Gondwana in their non-angiospermous dominants (Smiley, 1970; Li & Liu, 1994; Racey & Goodall, 2009). In South China, *Clavatipollenites* and tricolpates have been reported from presumed pre-Albian beds, plus tricolpates and tricolporates from the Albian-early Cenomanian (Li & Liu, 1994), but age control is poor.

The dynamics of relations between Southern Laurasia and Northern Gondwana are becoming increasingly clear. In England, Kemp (1968) reported the first tricolpates (with reticulate sculpture) in the marine early Albian, together with the distinctive *Clavatipollenites rotundus* group. Similarly, in well-dated Barremian through middle Albian marine sequences in Portugal, Heimhofer *et al.* (2007) found the first reticulate tricolpates and *C. rotundus* in the earliest Albian, joined later in the early Albian by striate tricolpates. Reticulate and striate tricolpates also occur in the late early Albian of Texas (Tanrikulu *et al.*, 2017). In the Potomac Group, reticulate tricolpates and *C. rotundus* appear consistently in upper Zone I (Doyle & Robbins, 1977; Hickey & Doyle, 1977). However, Hughes & McDougall (1990) illustrated exceedingly rare earlier tricolpates (one grain in the late Barremian, one in the early Aptian), and Doyle (1992) reported two tricolpate grains in lower Zone I (presumably Aptian).

Although these data imply that very rare eudicots existed in Southern Laurasia since the late Barremian, the consistent early Albian appearance of reticulate and striate tricolpates, which occurred in Northern Gondwana since the late Barremian and early Aptian, respectively, appears to represent a major migrational influx of eudicots, possibly due to global warming (Heimhofer *et al.*, 2005; Coiffard & Gomez, 2012; Zhang *et al.*, 2018). The Potomac leaf record shows a consistent pattern. Zone I contains rare simple angiosperm leaves comparable

to members of the ANITA grade, Chloranthaceae, magnoliids, and monocots, plus ternately lobed leaves. The latter have been compared with the basal eudicot order Ranunculales (see Jud, 2015), but the low number of vein orders, presence of mesophyll secretory cells, and absence of tricolpate pollen at some localities have led to suspicions that some of these leaves may not be crown-group eudicots (Doyle, 2012; Doyle & Upchurch, 2014). By contrast, Zone II (middle and late Albian) shows a variety of new eudicot leaf types, as discussed below.

The record in Northern Laurasia (Siberia, Alaska, Canada) and Southern Gondwana (southern South America, southern Africa, India, Australia, Antarctica) completes this picture by showing a still more delayed entry of angiosperms. In western Canada, tricolpates are first reported in the middle or late Albian (Norris, 1967; Playford, 1971; Singh, 1975). Angiospermous monosulcates appear at the same horizons or slightly earlier (early middle Albian: Playford, 1971). In Arctic Canada and Alaska, Brenner (1976) found no tricolpates until the Cenomanian, but they have been extended down into the late Albian in the Canadian Arctic Archipelago; angiospermous monosulcates are usually absent (Galloway *et al.*, 2012). In Australia, *Clavatipollenites* appears in the (Barremian?) Aptian, reticulate tricolpates in the middle or late Albian (Dettmann, 1973, 1986; Burger, 1993; Korasidis *et al.*, 2016). In southern Argentina, *Clavatipollenites* and other angiosperm monosulcates occur in the Aptian and are joined by tricolpates in the early Albian (Archangelsky *et al.*, 2009; Llorens & Perez Loinaze, 2016; Perez Loinaze *et al.*, 2016). In the Antarctic peninsula, *Clavatipollenites* appears in the early Albian and tricolpates in the middle Albian-Cenomanian (Dettmann & Thomson, 1987).

These variations do not contradict the congruence of the sequence of fossil pollen types and ideas on evolution based on extant plants; they simply mean that certain lines immigrated later into some areas. The earlier absences of angiosperms are not a function of absence of suitable rocks, since there are older sediments in many of these areas with rich pollen and spore floras but no reported angiosperms (e.g., white circles in Fig. 2).

Phylogenetic implications of pre-Aptian fossils. A phylogenetic perspective helps to clarify what Cretaceous fossils do and do not say about the early history of angiosperms. Because a single sulcus is presumably ancestral in angiosperms, being shared with other seed plants and inferred to extend down to the crown node on molecular trees (Fig. 1), other characters are

needed to infer whether monosulcate pollen represents crown-group angiosperms rather than stem relatives or unrelated gymnospermous groups. Columellar exine structure is evidence for a relationship to angiosperms rather than other taxa, but it does not distinguish between crown group members and stem relatives.

A character that may place fossils above the crown node is a reticulate tectum, seen from the Valanginian onward. This is because the first two angiosperm lines to diverge in most molecular trees, *Amborella* and Nymphaeales, have columellae (reduced to short connections between the tectum and the nexine in *Amborella*, crushed during development in some Nymphaeales: Doyle, 2005) but a continuous or microperforate tectum, whereas the third line, Austrobaileyales, has a reticulate tectum, which is also basic in mesangiosperms. In terms of parsimony (Doyle, 2005; Fig. 1), this implies that a reticulate tectum is a synapomorphy of Austrobaileyales and mesangiosperms, and that Valanginian reticulate-columellar monosulcates are nested in the crown group. However, some molecular analyses group *Amborella* and Nymphaeales as a clade (e.g., Barkman *et al.*, 2000; Xi *et al.*, 2014), in which case the ancestral tectum could be either continuous or reticulate. Furthermore, it is possible that in this case parsimony reconstruction is confounded by long-branch effects (where the length of a branch is the product of its duration in time and the rate of evolution), which might be corrected by model-based approaches (cf. Coiro *et al.*, 2018). In terms of time, *Amborella* is at the end of a very long branch, on which the tectum character might have more likely changed than on shorter branches, unless its rate of evolution was very low. Finally, monosulcate pollen adhering to the early Albian nymphaealean flower *Monetianthus* (Friis *et al.*, 2009b) is reticulate. However, because no stamens are preserved, it is uncertain that this pollen is from the same species.

Despite these uncertainties, there is reason to think that many (if not all) Cretaceous reticulate monosulcates and related pollen types belong to the crown group. One type that shares especially distinctive synapomorphies with a modern clade consists of tetrads of monoporate pollen called *Walkeripollis*, from the late Barremian of Gabon (Doyle *et al.*, 1990). Phylogenetic analysis links *Walkeripollis* with Winteraceae (Doyle & Endress, 2010), which are nested within Magnoliidae, the third-largest of the five mesangiosperm clades.

Other Hauterivian-Barremian pollen types resemble pollen found in stamens or on stigmas of younger mesofossils that are confidently linked with extant clades. For example, pollen of the *Clavatipollenites* type, with supratectal spinules and a sculptured sulcus, is associated with early Albian flowers that are nested in Chloranthaceae (*Canrightiopsis*: Friis *et al.*, 2015; Doyle & Endress, 2018). Similar pollen without spinules was produced by *Canrightia*, apparently a stem relative of Chloranthaceae (Friis & Pedersen, 2011; Doyle & Endress, 2014, 2018). *Similipollis*, with finer sculpture at the proximal pole and the sulcus margins, is associated with Albian mesofossils (*Anacostia*: Friis *et al.*, 1997) that phylogenetic analyses nest within Austrobaileyales (Doyle & Endress, 2014).

An intriguing case is the continuous-tectate genus *Tucanopollis*, from the Barremian-Aptian of Brazil (Regali, 1989) and Gabon/Congo (Doyle *et al.*, 1977; Doyle & Hotton, 1991) and the Hauterivian-Barremian of England (Hughes, 1994). It is similar to pollen of the Cenomanian genus *Pseudoasterophyllites*, a presumed halophyte with reduced leaves, which has been linked with *Ceratophyllum* and Chloranthaceae on molecular trees in which these taxa form a clade (Kvaček *et al.*, 2016). The floating aquatic *Montsechia*, from the Barremian of Spain, has also been associated with *Ceratophyllum* (Gomez *et al.*, 2015), but its pollen is unknown.

Despite being dominated by rather nondescript reticulate monosulcate pollen, the pre-Aptian fossil record clearly indicates significant diversification of crown-group angiosperms, some 10-15 Ma of which is represented in the pollen record. The most dramatic macromorphological divergence may be the extreme vegetative and floral reduction in *Montsechia* (Gomez *et al.*, 2015), but we see no way to estimate how much time this required, especially if reduction in aquatic lines can be unusually rapid (Cook, 1999).

These observations do not necessarily mean that all pre-Aptian angiosperm-like fossils belong to the crown group; some could be persisting stem relatives. The aquatic plant *Archaefructus* from the Barremian-Aptian Yixian Formation of China, with ternately dissected leaves and fertile structures of controversial morphology, was proposed as such by Sun *et al.* (2002). Later analyses linked it with Nymphaeales or eudicots (Doyle, 2008; Endress & Doyle, 2009), but its position remains highly uncertain (Friis *et al.*, 2011; Doyle & Endress, 2014). Another candidate is *Afropollis* (late Barremian to Cenomanian; Doyle *et al.*,

1982, 1990), which has a reticulate tectum but a gymnosperm-like laminated endexine, and which Friis *et al.* (1999, 2011) reported in microsporangia that lack angiosperm features.

Implications of the post-Barremian record. So far, there is no clear Barremian evidence for monocots, the second-largest of the five mesangiosperm clades. However, there are monocot fossils in the Aptian, including monosulcate pollen with a distinctive graded sculpture pattern (*Liliacidites*) and leaves with apically fusing venation (*Acaciaephyllum*) from lower Zone I of the Potomac Group (Doyle *et al.*, 2008), and vegetative remains representing the near-basal monocot family Araceae from the late Aptian Crato Formation of Brazil (Coiffard *et al.*, 2013).

Several other basically monosulcate clades are known from flowers and associated leaves and stems from the Aptian, Albian, and early Cenomanian. Nymphaeales are represented by *Pluricarpellatia* from the Crato Formation (Mohr *et al.*, 2008) and *Monetianthus* (Friis *et al.*, 2009b) from Portugal (early Albian: Heimhofer *et al.*, 2007; Doyle & Endress, 2014; Tanrikulu *et al.*, 2017). Among Magnoliidae, *Endressinia* and *Schenkeriphyllum* (Crato) are nested in Magnoliales (Doyle & Endress, 2010; Mohr *et al.*, 2013), while *Archaeanthus* (late Albian-early Cenomanian; Dilcher & Crane, 1984) is near or in Magnoliaceae (Doyle & Endress, 2010). Laurales include *Virginianthus* (middle Albian; Friis *et al.*, 1994) near the base of the order and *Mauldinia* (early Cenomanian; Drinnan *et al.*, 1990) linked with the derived families Lauraceae and Hernandiaceae (Doyle & Endress, 2010). Piperales are represented by *Hexagyne* (Crato; Coiffard *et al.*, 2014).

Like the appearance of monosulcate before tricolpate angiosperm pollen, the stratigraphic succession of tricolpate and derived pollen types is consistent with evolutionary transformation series proposed by earlier botanists (e.g., Takhtajan, 1959) and confirmed by molecular analyses (Doyle, 2005). A series of "basal eudicot" lines with basically tricolpate pollen diverge below the huge Pentapetalae or "core eudicot" clade, which is united by pentamerous flowers with differentiated sepals and petals. Pentapetalae consist of two large clades, Rosidae and Asteridae, and several smaller clades. Tricolporate pollen is apparently ancestral in rosids and asterids, but it also originated independently in some basal eudicots (Sabiaceae, Buxaceae, Menispermaceae), while both tricolpate and tricolporate pollen occurs in basal Pentapetalae such as Saxifragales, Dilleniaceae, and Caryophyllales (Furness *et al.*, 2007).

The derived status of the tricolporate condition is consistent with the fact that the oldest known tricolporate pollen is much younger than the first tricolpates. Tricolpate pollen with weakening at the middle of the colpi (tricolporoidate) first occurs in the middle Albian and becomes common in the late Albian, while types with more distinct ora appear in the latest Albian and Cenomanian. Many tricolporates show shifts from reticulate sculpture to a smooth tectum and triangular shape (Doyle, 1969; Pacltová, 1971; Herngreen, 1973; Laing, 1975; Singh, 1975; Doyle & Robbins, 1977; Burger, 1993; Horikx *et al.*, 2016; Perez Loinaze *et al.*, 2016).

Potomac Zone II and middle and late Albian beds in Kansas (Huang & Dilcher, 1994), Spain (Sender *et al.*, 2016), and Kazakhstan (Vakhrameev, 1952) contain abundant leaves and flowers related to basal eudicot lines (see Doyle & Endress, 2010). These include peltate leaves (*Nelumbites*) and floral receptacles related to *Nelumbo* (Upchurch *et al.*, 1994) and pinnately to palmately lobed leaves (*Sapindopsis*, platanoids) and heads of unisexual flowers related to *Platanus* (Friis *et al.*, 1988, 2011; Crane *et al.*, 1993), both in Proteales. Flowers with striate tricolpate pollen (*Spanomera*: Drinnan *et al.*, 1991) represent stem relatives of Buxaceae. *Kajanthus*, from the early Albian of Portugal (Mendes *et al.*, 2014), has been linked with Lardizabalaceae in the order Ranunculales, which is sister to all other eudicots.

The oldest clear megafossil record of Pentapetalae is *Dakotanthus*, a pentamerous flower with differentiated calyx and corolla, two cycles of five stamens, and tricolporate pollen from the latest Albian of Nebraska (Manchester *et al.*, 2018). This is followed by *Caliciflora* in the early Cenomanian of Maryland (Friis *et al.*, 2016). Flowers representing several clades of rosids and asterids are known from the younger upper Raritan Formation of New Jersey (Crepet, 2008).

The next conspicuous event in the pollen record is the appearance of triangular triporate pollen of the Normapolles group in the middle Cenomanian (Pacltová, 1971). Such pollen proliferates later in the Cretaceous of Europe and eastern North America (Góczán *et al.*, 1967; Batten, 1981). The pores have a compound structure, consistent with derivation from triangular tricolporate pollen by shortening of the colpi (Doyle, 1969). Early comparisons with triporate pollen in the rosid order Fagales are confirmed by association of Normapolles with fagalean flowers (Friis, 1983; Friis *et al.*, 2006). Triangular triporate pollen (*Triorites*

africaensis) also appears in the Cenomanian of Northern Gondwana (Jardiné & Magloire, 1965; Herngreen, 1973), but it appears to be related to Proteaceae in the basal eudicot order Proteales (Ward & Doyle, 1994). The pores are simple, consistent with origin from tricolpate pollen, as expected from the position of Proteaceae.

General evolutionary implications. Perhaps more than the record of angiospermous monosulcates, the stratigraphic record of tricolpate and derived pollen types argues against the long period of unrecorded diversification implied by molecular dating analyses. This is illustrated graphically by Fig. 4, based on a dated molecular tree derived from the data set of Magallón *et al.* (2015), which is representative of trees with a Triassic age of angiosperms. In this analysis we estimated the number of lineages with sulcate, colpate (mostly tricolpate), colporate, porate, and inaperturate pollen from states in living taxa using stochastic character mapping (see Methods S1 and Table S1), juxtaposed with observed curves of pollen types in three Cretaceous sections. Estimated ages center on 220 Ma for angiosperms (Late Triassic), 150 Ma for eudicots (Late Jurassic), and 132 Ma for Pentapetalae (Hauterivian), comparable to dates of Barba-Montoya *et al.* (2018). The tree implies that colpates were already nearly as diverse as sulcates when they are first observed as fossils in the late Barremian, and more remarkably that colporates were as diverse as colpates, ca. 20 Ma before the first tricolporate pollen is seen in the late Albian. It is difficult to attribute this mismatch to failure of palynologists to recognize earlier tricolpate and tricolporate pollen. It is possible to overlook monosulcate angiosperm pollen, which may require close examination to distinguish from gymnospermous pollen, but tricolpates and tricolporates are easily recognized, and palynologists have been aware of their relation to angiosperms since early in the history of the field.

These considerations show paradoxical congruence relations among molecular phylogenetic analyses, molecular dating, and the fossil record. The stratigraphic succession of pollen types is congruent with scenarios for character evolution inferred from molecular phylogenetics, but not with molecular dating analyses. Congruence between inferred pollen evolution and stratigraphy is expected only if there was a relatively short lag between evolution of successively more derived types and their appearance in the fossil record. If molecular dates of the sort in Fig. 4 are correct, one must ask why taxa with new pollen types waited patiently for tens of millions of years before entering the fossil record in the order they had evolved.

A related question is why angiosperms did not radiate in the Jurassic if they originated then, given that they expanded so dramatically in the Cretaceous. The answer cannot be that the whole suite of angiosperm innovations had not yet accumulated, because in that case Jurassic representatives of the angiosperm line would be on the stem lineage rather than in the crown group, and the conflict with molecular dates would remain. It is difficult to imagine extrinsic environmental factors that might have suppressed radiation of angiosperms as a whole, considering how quickly they occupied a wide range of climatic belts and local habitats in the Cretaceous (Doyle & Donoghue, 1993). However, as argued by Feild *et al.* (2004), if Late Jurassic angiosperms were like extant terrestrial members of the ANITA grade (*Amborella*, Austrobaileyales), which grow mainly in wet tropical to subtropical forest understory habitats, they might have been restricted geographically and inhibited from diversifying because most of the tropical belt was arid at that time. The observed Cretaceous rise of angiosperms might then represent the radiation of mesangiosperms. There are some Early Cretaceous fossils from the ANITA grade, such as *Anacostia*/*Similipollis* in Austrobaileyales (Friis *et al.*, 1997; Doyle & Endress, 2014) and a growing number of Nymphaeales. However, *Similipollis* is a minor element in palynofloras, and it is possible that the nymphaealean line was still terrestrial in the Jurassic and did not become widespread until it later invaded aquatic habitats (Doyle & Endress, 2014).

Potential taphonomic biases. Barba-Montoya *et al.* (2018) suggested that the mismatch between fossil and molecular dates "may be more perceived than real" because the "orderly and incrementally phased environmental invasion… may be an artefact imposed by the non-uniformity of the rock record." However, this argument refers to models for the ecological radiation of angiosperms proposed by Hickey & Doyle (1977) and Coiffard *et al.* (2012), based on sedimentary facies associations and functional morphology of fossil leaves, not the patterns stressed here. There is indeed a danger that taphonomic biases may affect some inferences, such as the argument that the predominance of aquatic angiosperms in the Barremian supports an aquatic origin (Coiffard *et al.*, 2012; see Box 2). It is possible that aquatic angiosperms are overrepresented in the Barremian and Aptian record because of intense attention to the justly famous lacustrine deposits at Las Hoyas, the Yixian Formation, and the Crato Formation, while other facies with less well-preserved remains are unstudied.

By contrast, because palynological studies sample a variety of fluvial, deltaic, and nearshore marine facies, and because pollen is readily transported by wind and water, the pollen record

should give a more comprehensive qualitative view of the angiosperm flora at a given time, as argued by Muller (1970). Judging from studies on the Potomac Group (Doyle, 1969; Doyle & Robbins, 1977; Hickey & Doyle, 1977), which was deposited mainly in a meandering fluvial system, certain angiosperm pollen types are much more common in some samples than in others, presumably because of local abundance of the source plants in particular floodplain habitats. However, there is a relatively uniform lower-frequency "background" assemblage of angiosperms common to most samples, which presumably includes pollen transported from many habitats. Angiosperm leaves show much more facies restriction, a fact exploited by Hickey & Doyle (1977) in reconstructing ecological preferences. All pollen in the intensively studied nearshore marine sequence in Portugal (Heimhofer *et al.*, 2007; Horikx *et al.*, 2016) is transported, doubtless from a broad spectrum of inland environments.

III. Pre-Cretaceous angiosperm reports

There is a long history of reports of pre-Cretaceous angiosperms and their rejection for stratigraphic or morphological reasons (Axelrod, 1952, 1970; Scott *et al.*, 1960; Hughes, 1961a; Doyle, 2012; Herendeen *et al.*, 2017; Wang, 2018). Recently, molecular dating studies have cited putative pre-Cretaceous angiosperms as support for early molecular ages for crown-group angiosperms (e.g., Barba-Montoya *et al.*, 2018), and paleobotanists have taken molecular dates as enhancing the plausibility of pre-Cretaceous claims (e.g., Liu & Wang, 2017; Wang, 2018). It should be recalled that fossils relate to molecular ages of the angiosperms only if they belong to the crown group; stem relatives can be either older or younger than the crown node.

Barba-Montoya *et al.* (2018) suggested that paleobotanical arguments against pre-Cretaceous angiosperms are flawed because of reliance on absence of evidence for "key characters," rather than evidence of their absence; formulation of key characters in "the increasingly outmoded parsimony-based phylogenetic framework"; and methodological biases in distinguishing stem- and crown-angiosperms. However, these issues are irrelevant in most cases. Bayesian inference performs better than parsimony in cases of long-branch attraction, but it would be unwarranted to dismiss results based on parsimony out of hand: both methods usually give congruent results with empirical data sets (Rindal & Brower, 2011; Coiro *et al.*, 2018). No putative pre-Cretaceous angiosperms have been examined in an explicit phylogenetic framework of any sort (although parsimony was used to evaluate the putative

Cretaceous stem fossil *Archaefructus*: Sun *et al.*, 2002; Doyle, 2008), and there are few cases where the issue is whether fossils are stem relatives or crown-group members. Usually disagreement concerns whether morphological features were misinterpreted, or whether the fossils are related to other seed plant groups. Some have defined angiosperms typologically (plants with enclosed seeds) while neglecting evidence for the homology of the structures involved or characters of other organs. There are similar problems with some Cretaceous fossils (see Herendeen *et al.*, 2017), but here we focus on pre-Cretaceous records (for more details of our interpretations of particular taxa, see Notes S1).

Several fossils cited by Axelrod (1952) and others as pre-Cretaceous angiosperms were later shown to belong to other plant groups that were unrecognized at the time. A classic example is *Eucommiidites*, a Jurassic and Cretaceous pollen type with three furrows that Erdtman (1948) compared with the tricolpate pollen of eudicots. Confirming earlier less conclusive indications (e.g., Couper, 1958; Doyle *et al.*, 1975), Pedersen *et al.* (1989) and Friis *et al.* (2009a) associated *Eucommiidites* with male and female structures that they assigned to the new order Erdtmanithecales, which is apparently related to Gnetales.

A recent example of this sort is *Schmeissneria*, described from the Early Jurassic of Germany by Kirchner & van Konijnenburg-van Cittert (1994) as a ginkgophyte. It has short shoots bearing strap-shaped leaves with an even number of veins; attached female axes bearing units consisting of one or two seeds surrounded by a longitudinally ridged "cupule"; and male axes bearing sporophylls with a cluster of pollen sacs, which are not known attached but occur consistently in the same beds. Wang *et al.* (2007) and Wang (2010, 2018) reinterpreted the female units in the German fossils and Middle Jurassic material from China as flowers with a perianth and two fused carpels with enclosed ovules. Wang *et al.* (2007) rejected the ginkgophyte interpretation because Kirchner & van Konijnenburg-van Cittert (1994) had excluded *Schmeissneria* from all known ginkgophyte genera; however, this only meant it was a new genus and in no way excluded it from ginkgophytes as a whole, which it resembles in all the vegetative and male features listed. To this list van Konijnenburg-van Cittert (2010) added smooth monosulcate pollen, which is typical of (though not limited to) ginkgophytes. Furthermore, the female units can be reinterpreted in ginkgophytic terms, with the carpels as seeds (with apical hairs, as argued by Wang, 2010), and the supposed enclosed seeds, which show no regular relation to the ridges of the cupule and no cellular detail, as resin bodies in the cupule wall. The cupule may correspond to the bivalved capsule of the ginkgophytic

order Czekanowskiales, which differs in containing several seeds rather than one or two. Wang *et al.* (2007) and Wang (2010) described the female structures as having two locules separated by a septum, but identification of such internal features often requires three-dimensional preservation, whereas these fossils are nearly two-dimensional compressions. The reconstruction of *Schmeissneria* presented by Wang (2018) is most un-angiosperm like, but it closely conforms to the morphology of a ginkgophyte group such as Czekanowskiales.

A similar case is *Solaranthus*, from the Middle Jurassic of China, which Zheng & Wang (2010) interpreted as a flower with numerous carpels on a peltate receptacle and reflexed tepals and stamens. Deng *et al.* (2014) synonymized *Solaranthus* with *Aegianthus* (a resemblance already noted by Zheng & Wang, 2010), which has peltate microsporophylls with pollen sacs below the polygonal cap and resin bodies in the cap. They considered *Aegianthus* a cycad, but because its microsporophylls are nearly radial, while those of cycads are bilateral, a more likely relationship may be with the "seed fern" order Peltaspermales. The smooth monosulcate pollen would be consistent with either affinity. The supposed carpels appear to be resin bodies in the cap, while the stamens and tepals are clearly pollen sacs viewed at various angles. Their reflexed orientation would be typical for cycad or peltasperm pollen sacs but bizarre for parts of a flower. Wang (2018) discounted the interpretation of Deng *et al.* (2014) but offered no additional evidence for *Solaranthus* being anything other than a gymnosperm pollen organ.

Liu & Wang (2016) described *Euanthus* from the Middle Jurassic of China as a flower with sepals, petals, anthers, and a gynoecium with an apical style and pentamerous ovary. However, the texture of the supposed sepals and petals is distinctly woody, more like the cone scales of a conifer than perianth parts of an angiosperm, as illustrated graphically by Herendeen *et al.* (2017). The style may represent the cone axis where scales have fallen off, but it is not clear whether it is actually part of the specimen or just underlies it. The pentamerous receptacle appears to be a basal view of the broken cone axis and surrounding smaller scales, while the so-called anthers (Liu & Wang, 2016; Wang, 2018) have no clear morphological features. Overall, *Euanthus* is more readily interpreted as a fragmentary conifer cone than an angiosperm flower.

A similar case may be *Nanjinganthus* from the Early Jurassic of China (Fu *et al.*, 2018), known as numerous compressions with a "perianth" of appendages similar to those of

Euanthus, with ridges suggesting robust vascular bundles. Ten specimens have a branched prolongation of the axis described as a "dendroid style." This resembles an axis with spirally arranged appendages more than the style of any angiosperm. It recalls the male cones of some conifers, which have basal bracts resembling the "perianth." Fu *et al.* (2018) rejected this interpretation because they found no pollen on the dendroid structure, but this could be due to loss at many points prior to burial. Alternatively, the "style branches" may be degraded ovuliferous scales of a female conifer cone. Fu *et al.* (2018) interpreted the basal part of the fossils as an inferior ovary with 1-3 enclosed ovules, but the morphology of this area is obscure because of poor preservation and irregularity in the number and appearance of the supposed ovules.

Other proposed pre-Cretaceous angiosperms are less clearly related to any particular non-angiospermous group but show little evidence of homologies with angiosperm structures, or have anomalous features that cast doubt on such homologies. One is *Xingxueanthus*, from the Middle Jurassic of China (Wang & Wang, 2010; Wang, 2018), interpreted as an axis with bracts and axillary gynoecia with free-central placentation. However, the supposed axis of the flower (placenta) is perpendicular to the bract and parallel to the axis, not at an angle arising from the axil. The presence of a bract subtending the "gynoecium" and the woody appearance of the "placenta" could indicate that this fossil represents the ovuliferous shoot of a coniferophyte, but again it is highly compressed, and the morphological nature of its parts is obscure.

Two other fossils from the Middle Jurassic of China have herbaceous leafy stems. Han *et al.* (2016) described *Juraherba* as consisting of a corm-like stem bearing roots, linear one-veined leaves, and axes terminating in longitudinally ridged fructifications that contain seeds. One-veined leaves occur in a few angiosperms, such as Hydatellaceae in the Nymphaeales (as noted by Han *et al.*, 2016), but they are more typical of lycophytes and conifers. The ridges appear to be narrow pointed appendages of a strobilus; the supposed seed lacks any visible structure. *Yuhania* (Liu & Wang, 2017) consists of a stem bearing linear leaves with 5-6 parallel veins and structures described as aggregate fruits. However, the putative fruits vary in size by an order of magnitude, and the one with the most visible structure (fig. 2h) is not clearly attached. Liu & Wang (2017) and Wang (2018) interpreted the units making up the fruits as carpels subtended by bracts (contrary to the definition of an aggregate fruit as derived from one flower with free carpels), but the supposed bracts and carpels have a highly

anomalous reflexed orientation, and the structures identified as seeds have no visible morphology. Better preserved specimens of these enigmatic plants are required to obtain enough detail for robust systematic conclusions.

A somewhat similar case is *Sanmiguelia*, originally based on pleated leaves from the Late Triassic of Colorado (Brown, 1956). Cornet (1986, 1989) associated Late Triassic leaves from Texas with woody stems and male and female structures, the latter as interpreted as flowers with a perianth and several carpels. He argued that the leaves are monocot-like in having two orders of parallel venation and cross-veins, but the low frequency and irregularity of the cross-veins suggest they may be artifacts of degradation and shredding of leaf tissue. The male organs are strobili that appear more ginkgophytic than angiospermous; the pollen is smooth and monosulcate, consistent with many possible affinities. The female organs are so highly compressed that features such as enclosed seeds are not demonstrable (Doyle & Donoghue, 1993). The leaf morphology might be most plausibly derived from a coniferophyte (ginkgophyte, conifer, gnetophyte) type with an even number of parallel veins.

A general problem is that the proposed Jurassic angiosperms known as isolated reproductive structures (*Solaranthus*, *Euanthus*, *Nanjinganthus*, *Xingxueanthus*) occur in compression floras that are rich in typical Jurassic ferns, ginkgophytes, cycadophytes, and conifers (e.g., Na *et al.*, 2017; Pott & Jiang, 2017; Fu *et al.*, 2018) but contain no leaves with distinctive angiosperm apomorphies (several orders of reticulate venation, etc.), while those known as nearly whole plants (*Schmeissneria*, *Juraherba*, *Yuhania*) have leaves with no angiosperm features. By contrast, in Cretaceous and Cenozoic impression and compression floras, flowers are far less common than leaves of the same taxa. If the Jurassic fossils were angiosperm stem relatives they might not have typical angiosperm leaves, but they would also have no bearing on molecular ages. Furthermore, one would expect angiosperms to be more like each other in the Jurassic than in the Early Cretaceous, but if anything proposed Jurassic angiosperms are more disparate morphologically and lack common features that might provide a coherent picture of the first angiosperms.

There are pre-Cretaceous fossils that share clearer potential synapomorphies with angiosperms. These include the Late Triassic Crinopolles pollen group, first described by Cornet (1989) from the Newark sequence of Virginia, which includes monosulcate pollen with columellae and a reticulate tectum. However, in well-preserved specimens, TEM shows

that the nexine consists of laminated endexine of uniform thickness (Cornet, 1989; Doyle & Hotton, 1991; Fig. 5a-d), as in gymnospermous pollen, whereas in Early Cretaceous and extant monosulcate angiosperms endexine is either lacking or non-laminated, except under the sulcus (Doyle *et al.*, 1975). This could mean that Crinopolles represent either a convergent gymnospermous group or angiosperm stem relatives. As discussed above, it is not resolved whether the ancestral tectum in angiosperms was continuous or reticulate. Reticulate-columellar monosulcates are also known from the Middle Triassic of the Barents Sea and Switzerland (Hochuli & Feist-Burkhardt, 2004, 2013), but their nexine structure is unknown.

Equally tantalizing is *Phyllites* sp. of Seward (1904) from the Middle Jurassic Stonesfield Slate of England (see also Cleal & Rees, 2003; Fig. 5e,f). This is a single ovate leaf with acrodromous venation (palmate venation with a midvein and arcuate lateral primary veins). Unfortunately no cuticle or finer venation is preserved, so it is not known if there were several orders of reticulate veins. The major venation suggests a position in the crown group, since in terms of parsimony ovate leaf shape is ancestral but palmate venation is derived, arising in Nymphaeales, Piperales, some Laurales, and eudicots (Doyle, 2012).

IV. Potential biases in molecular dating

This survey indicates that the angiosperm fossil record is indeed difficult to reconcile with molecular analyses that date the angiosperm crown group as much older than the Cretaceous, and the conflict cannot be readily explained as a result of misinterpretation of the fossil record. Molecular dating analyses have sometimes been perceived as more trustworthy, because they supposedly overcome biases and weaknesses of the fossil record (e.g., Kenrick, 2011). However, molecular dating methods are not free from their own potential sources of bias, and not necessarily as accurate as desired, or as robust against violation of their many assumptions (Bromham *et al.*, 2018).

Cases in which molecular analyses estimate a much older age than fossil evidence in other groups, such as mammals (dos Reis *et al.*, 2012; O'Leary *et al.*, 2013; Phillips & Fruciano, 2018), have led others to reinvestigate the assumptions of molecular dating. Indeed, even though new methods to deal with issues such as rate heterogeneity and topological error are

constantly being developed, it could be that some biological problems are still outside the scope of our current implementations.

Many Bayesian studies dealing with the age of the angiosperms have tested the sensitivity of molecular dates to different prior assumptions or partitioning schemes (Foster *et al.*, 2016; Barba-Montoya *et al.*, 2018). However, other authors have directly investigated systematic biases that could lead to overestimation of the age of the angiosperms. Beaulieu *et al.* (2015) used a simulation approach to detect potential biases created by molecular rate heterogeneity linked to habit (herbaceous vs. woody), as well as by the diversified sampling strategy necessarily employed in such a large group. Their results demonstrated that even for sequences generated on a simulated tree of angiosperms with a young crown-group age (140 mya), relaxed-clock methods tended to overestimate the age of the crown group by as much as 70 my when high-rate, herbaceous clades are present near the base of the group. More puzzlingly, the age of the crown angiosperms was overestimated by 50 my even when simulations were conducted under favorable conditions for relaxed-clock methods.

Another explanation for this perplexing phenomenon was offered by Brown & Smith (2018), who identified a substantial issue with the implementation of node priors: the interaction between the many different user-defined priors and the topology generated effective priors that pushed the ages towards a much older origin of crown-group angiosperms than expected from the user-specified priors.

These methodological and biological complications have been identified in placental mammals, where the fossil record suggests an explosive radiation in the Paleocene and only stem relatives are known from the Cretaceous, but molecular analyses place the radiation well back in the Late Cretaceous. In this case, Phillips & Fruciano (2018) identified a connection between the use of calibrations at the base of clades that show parallel shifts towards slow molecular rates (primates, proboscidians) and older inferred ages for crown placentals. Two clades used for calibration in angiosperms, Proteales and Fagales, may represent similar cases, since they both have unusually short branches on molecular phylograms.

These considerations could mean that the tempo and mode of molecular evolution during the origin and early radiation of the angiosperms are extremely hard to model. A deeper investigation of the implications of fossil-informed ages for the mode of molecular evolution

in angiosperms could provide novel insights not only on the time of their origin, but also on mechanisms acting at the molecular level during their radiation.

V. Conclusions

This survey reaffirms the view that stratigraphic and morphological patterns in the Cretaceous angiosperm record are difficult to reconcile with molecular dating analyses that place the origin of the group long before the Cretaceous. Reports of pre-Cretaceous angiosperms do not offer serious support for older molecular dates, and most are clearly erroneous. These results, like those involving other taxa such as placental mammals (Phillips & Fruciano, 2018), underline the need to investigate whether current molecular methods have inherent biases that are responsible for conflicts of this type with the fossil record.

The Cretaceous record permits and may even favor some Jurassic diversification of the angiosperms, and the nearly universal molecular support for a pre-Cretaceous origin should give pause to a literal reading of the known record. It would be unwarranted to dismiss scenarios in which low-diversity ANITA-grade angiosperms were ecologically and geographically restricted in the Jurassic, e.g., if they grew in wet tropical understory habitats like woody members of the ANITA grade (Feild *et al.*, 2004). In this case, the observed rise of reticulate monosulcate pollen beginning in the Valanginian might mark the radiation of mesangiosperms. However, the amount of pre-Cretaceous diversification implied by earlier Jurassic, Triassic, or Permian dates would conflict with the Cretaceous record, in which successive new pollen types appear in the order of evolution inferred from molecular phylogenetic analyses, but much later than predicted by molecular dating.

Our review demonstrates that the fossil record provides what appears to be fundamental evidence on the timescale and pattern of the origin and early evolution of angiosperms. This underlines the continued importance of expertise in paleobotany and related fields. Many of the erroneous interpretations of pre-Cretaceous fossils discussed here are due to misunderstandings of basic plant morphology. From the viewpoint of molecular dating alone, paleobotanical expertise is pivotal for successful calibration, especially now that the incorporation of fossil information using well-curated morphological matrices is becoming common practice in the broader field (Gavryushkina *et al.*, 2017). Furthermore, discovery of pre-Cretaceous crown-group angiosperm fossils would confirm molecular evidence that

angiosperms are older than their currently accepted record, but recognition of angiosperm stem relatives could be vastly more significant for understanding the origin of angiosperms and their distinctive features. Thus better evidence on venation or cuticle of leaves such as *Phyllites* from the Stonesfield Slate or association of Crinopolles pollen with other plant organs could result in major breakthroughs in angiosperm paleobotany. However, full use of this information would require a broad and deep perspective on plant morphology, anatomy, and taphonomy.

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Supplementary information captions

Methods S1: Methods for our reconstruction of Lineages-through-time producing different kinds of pollen used in Fig. 4.

Notes S1: Description and reinterpretation of supposed pre-Cretaceous angiosperms.

Table S1: Taxa coded for generating Fig. 4 and sources of the data.

Fig. 1 Timescale, simplified dated molecular phylogeny of angiosperms (based on data of Magallón *et al.*, 2015), and noteworthy Cretaceous angiosperm pollen types and possible pre-Cretaceous relatives placed at their level of appearance (most Cretaceous types continue into younger beds). Diagrammatic sketches of fossil pollen types in polar view (sizes of pollen grains and sculpture not to scale): (a) Triassic pollen of Hochuli & Feist-Burkhardt (2013); (b) Crinopolles group; (c) Valanginian-Hauterivian reticulate monosulcate; (d) *Tucanopollis*; (e) *Clavatipollenites*; (f) *Stellatopollis*; (g) *Similipollis* (dotted line indicates proximal area of fine sculpture); (h) *Afropollis*; (i) *Liliacidites*; (i) *Walkeripollis* tetrad; (k, l) reticulate tricolpates (*Tricolpites*, *Rousea*); (m) striate tricolpate (*Striatopollis*); (n) tricolporoidate (equatorial view); (o) smooth prolate tricolporate; (p) smooth triangular tricolporate; (q) Normapolles group (*Complexiopollis*); (r) *Triorites africaensis*. Gray arrows indicate delayed general appearance of tricolpates in Southern Laurasia. Tri, Triassic; Jur, Jurassic; Ber, Berriasian; Val, Valanginian; Hau, Hauterivian; Bar, Barremian; Apt, Aptian; Alb, Albian; Cen, Cenomanian.

Fig. 2 Geographic and migrational patterns in the early angiosperm record, illustrated by paleogeographic maps for four intervals in the Early Cretaceous (http://www.odsn.de/odsn/services/paleomap/paleomap.html), with locations of selected geological sequences containing early angiosperm pollen (see the 'Temporal and spatial patterns in the pollen record' subsection for discussion of selection criteria). Symbols indicate well-studied palynofloras with no reported angiosperm pollen, presence of monosulcate angiosperm pollen only, and presence of tricolpate (eudicot) pollen (as well as angiospermous monosulcates, except in Arctic Canada). When symbols are shown only for

younger horizons, this indicates a lack of older sediments (e.g. below the Potomac Group) or insufficient palynological study of older beds (e.g. Portugal). Ages for base maps: (a) 129.4 Ma (Hauterivian–Barremian boundary); (b) 125 Ma (Barremian–Aptian boundary); (c) 113 Ma (Aptian–Albian boundary); (d) 100.5 Ma (Albian–Cenomanian boundary). Data for Arctic Canada (Sverdrup Basin, Ellef Ringnes and Ellesmere Islands): Brenner (1976), Galloway *et al.* (2012); western Canada plains (Alberta, Saskatchewan, Manitoba): Norris (1967), Playford (1971), Singh (1975); Potomac Group, eastern USA (Delaware, Maryland, Virginia): Doyle & Robbins (1977); England (Wealden and overlying marine units, southern England): Kemp (1968), Laing (1975), Hughes (1994); Portugal (Lusitanian and Algarve Basins): Heimhofer *et al.* (2007); Italy (southern Tuscany): Trevisan (1988); Israel: Brenner (1996); Egypt (Mersa Matruh, Dakhla Oasis): Schrank (1983, 1992), Penny (1991), Ibrahim (2002), Schrank & Mahmoud (2002); northeastern Brazil (Recôncavo-Tucano and Sergipe-Alagoas Basins): Regali & Viana (1989); Gabon/Congo (northern Gabon and Republic of the Congo): Doyle *et al.* (1977, 1982), Doyle (1992); northern Patagonia, Argentina (Neuquén Province): Archangelsky *et al.* (2009); southern Patagonia, Argentina (Santa Cruz Province): Archangelsky *et al.* (2009), Llorens & Perez Loinaze (2016), Perez Loinaze *et al.* (2016); Antarctica (James Ross Island, Antarctic Peninsula): Dettmann & Thomson (1987); Queensland, Australia (Eromanga and Surat Basins): Burger (1993); Victoria, Australia (Otway Basin): Dettmann (1973, 1986), Korasidis *et al.* (2016). Val, Valanginian; Hau, Hauterivian; Bar, Barremian; Apt, Aptian; Alb, Albian.

Fig. 3 Time of appearance (yellow symbols) and persistence (colored lines) of monosulcate (blue) and tricolpate (purple) angiosperm pollen plotted against paleolatitude, based on the data summarized in Fig. 2. For simplicity, paleolatitudes are based on positions of localities at the Aptian-Albian boundary (113 Ma, Fig. 2c); in some areas, particularly Australia and Antarctica, localities shift considerably in paleolatitude through time (cf Fig. 2), but their early Albian latitudinal positions are close to those when each of the pollen classes appears. In England and the Potomac sequence, isolated earlier occurrences of tricolpate pollen (as opposed to consistent presence in most samples) are indicated by tricolpate symbols superimposed on the blue line. Tri, Triassic; Jur, Jurassic; Ber, Berriasian; Val, Valanginian; Hau, Hauterivian; Bar, Barremian; Apt, Aptian; Alb, Albian; Cen, Cenomanian.

Fig. 4 Comparison of temporal changes in diversity of lineages with pollen belonging to major classes predicted by a dated molecular tree and observed in the Early Cretaceous fossil record. Blue, sulcate (including monosulcate and derived pollen types, such as monoporate and sulculate); purple, colpate (including tricolpate, hexacolpate, and other presumably derived types); yellow, colporate (including tricolporate, tetracolporate, etc.); green, inaperturate; black, porate (including triporate, pantoporate, but not monoporate). Left, predicted number of lineages through time based on the data set of Magallón *et al.* (2015) analyzed without the Early Cretaceous constraint on the angiosperm crown node. For sources of pollen data and methods, see Supporting Information. Pie diagrams show the relative probabilities of the different states at the reconstructed node; their position on the *x*-axis corresponds to the number of nodes at a given horizon that share the same reconstructed state weighted by its probability (see Supporting Information for details). Right, curves of observed diversity of sulcate, colpate, and colporate angiosperm pollen 'species' through time in three geological sections. Numbers at each horizon represent the number of species of the pollen class whose observed ranges pass through the horizon, not the number of species in any one sample. Sources of data: Egypt, Mersa Matruh 1 well, Fig. 8 of Penny (1991), not including *Afropollis*; Portugal, Luz section (Algarve), Fig. 9 of Heimhofer *et al.* (2007); Potomac Group, Delaware City wells D12 and D13 (Delaware), Fig. 4 of Doyle & Robbins (1977). Numbers of species may not be directly comparable between sections due to the use of SEM by Penny (1991) vs light microscopy by Heimhofer *et al.* (2007) and Doyle & Robbins (1977), different levels of attention to fine differences among pollen types, and other factors. The mid-Aptian peak of monosulcates in Egypt may be exaggerated because of Penny's intensive study of the monosulcate *Pennipollis* group; declines in diversity at the top of the Egyptian and Portuguese sections may relate to decreasing sample richness and/or less intensive study. Dashed lines show downward extensions of monosulcate angiosperms within the same phytogeographic province, with the line below the curve for Egypt (Northern Gondwana) based on data from Italy (Trevisan, 1988) and Israel (Brenner, 1996), and the line below the curve for Portugal (Southern Laurasia) based on the Wealden of England (Hughes, 1994). The two breaks in curves in the Potomac sequence correspond to depositional hiatuses, the lower of which reflects thinning of the Aptian portion of the Potomac Group in Delaware. The later appearance of tricolpates in Portugal and the Potomac relative to Egypt illustrates their delayed northward migration across the Tethys (cf Figs. 2, 3). Tri, Triassic;

Jur, Jurassic; Ber, Berriasian; Val, Valanginian; Hau, Hauterivian; Bar, Barremian; Apt, Aptian; Alb, Albian; Cen, Cenomanian.

Fig. 5 Possible pre-Cretaceous angiosperms or angiosperm relatives. (a–d) Crinopolles pollen, Chinle Formation, Late Triassic, Arizona (Doyle & Hotton, 1991); (a, b) light micrographs, two focal levels; (c) scanning electron micrograph, proximal view; (d) transmission electron micrograph of flattened grain; e, endexine. (e, f) *Phyllites* sp. of Seward (1904), Stonesfield Slate, Middle Jurassic, England (Cleal & Rees, 2003), part and counterpart, courtesy of C. J. Cleal and The Palaeontological Association. Bars: (a, b) 10 µm; (c) 5 µm; (d) 1 µm; (e, f) 10 mm.

Box 1 Definitions of phylogenetic and palynological terms.

Crown group: the most recent common ancestor of a living clade and all its descendants, both living and fossil. All clades recognized in molecular analyses are crown groups.

Stem lineage: the evolutionary line connecting a crown group with its common ancestor with the most closely related living group (sister group).

Stem relative: an extinct group on or attached to the stem lineage.

Monosulcate: with a single elongate furrow-like polar aperture (sulcus) of thinner exine for pollen tube germination; the polar axis is defined by an imaginary line running through the center of the pollen grain and the center of the meiotic tetrad in which it was formed (see accompanying sketch of pollen tetrad and Fig. 1a–g).

Tricolpate: with three elongate furrow-like apertures (colpi, singular colpus) for pollen tube germination running along lines of longitude (relative to the polar axis as defined above; see accompanying sketch of pollen tetrad and Fig. 1k–m).

Tricolporate: with three colpi plus an internally differentiated pore or os (plural ora) in the middle of each colpus. The resulting apertures are described as compound (see Fig. 1n–p).

Triporate: with three round apertures. Pores may be simple or compound (with differentiated inner and outer apertures; see Fig. 1q,r).

Pantoporate, periporate, polyforate: with numerous round apertures scattered over the surface of the grain.

Disulculate, zonasulculate: with two furrows or one ring-like furrow, respectively, on or parallel to the equator.

Inaperturate: with no differentiated aperture (and usually a thin exine, in which the pollen tube can germinate at any point).

Box 2 Aquatic origin of angiosperms.

Coiffard *et al.* (2012) interpreted the abundance of aquatic angiosperms such as *Montsechia*, Nymphaeales, and *Archaefructus* in Barremian-Aptian lacustrine deposits as evidence that the angiosperms were originally aquatic. There is no question that aquatic habitats were among the first where angiosperms were abundant, but this does not necessarily mean they originated there. The position of aquatic clades in molecular phylogenies suggests rather that the aquatic habit was a specialization that arose in several early lines, namely Nymphaeales, *Ceratophyllum*, *Nelumbo* among eudicots, and monocots, in which the earliest-diverging line, *Acorus*, and basal members of the second line, Alismatales, are marsh plants. These lines are nested among groups of terrestrial plants with normal woody stems (*Amborella*, Austrobaileyales, Chloranthaceae, Magnoliidae). The stem anatomy of these terrestrial groups is difficult to explain if they were derived from aquatic ancestors, in which secondary growth is highly reduced or absent (Feild & Arens, 2007). Furthermore, given the wide geographic distribution of modern aquatic plants and the fact they usually grow in sites of sedimentary deposition, it seems difficult to explain how angiosperms could originate long before the Cretaceous and remain undetected if they were originally aquatic. Together, these arguments suggest that a better explanation for the Barremian-Aptian abundance of aquatics may be the higher probability of preservation of plants in lacustrine sedimentary environments than in contemporaneous drier habitats.

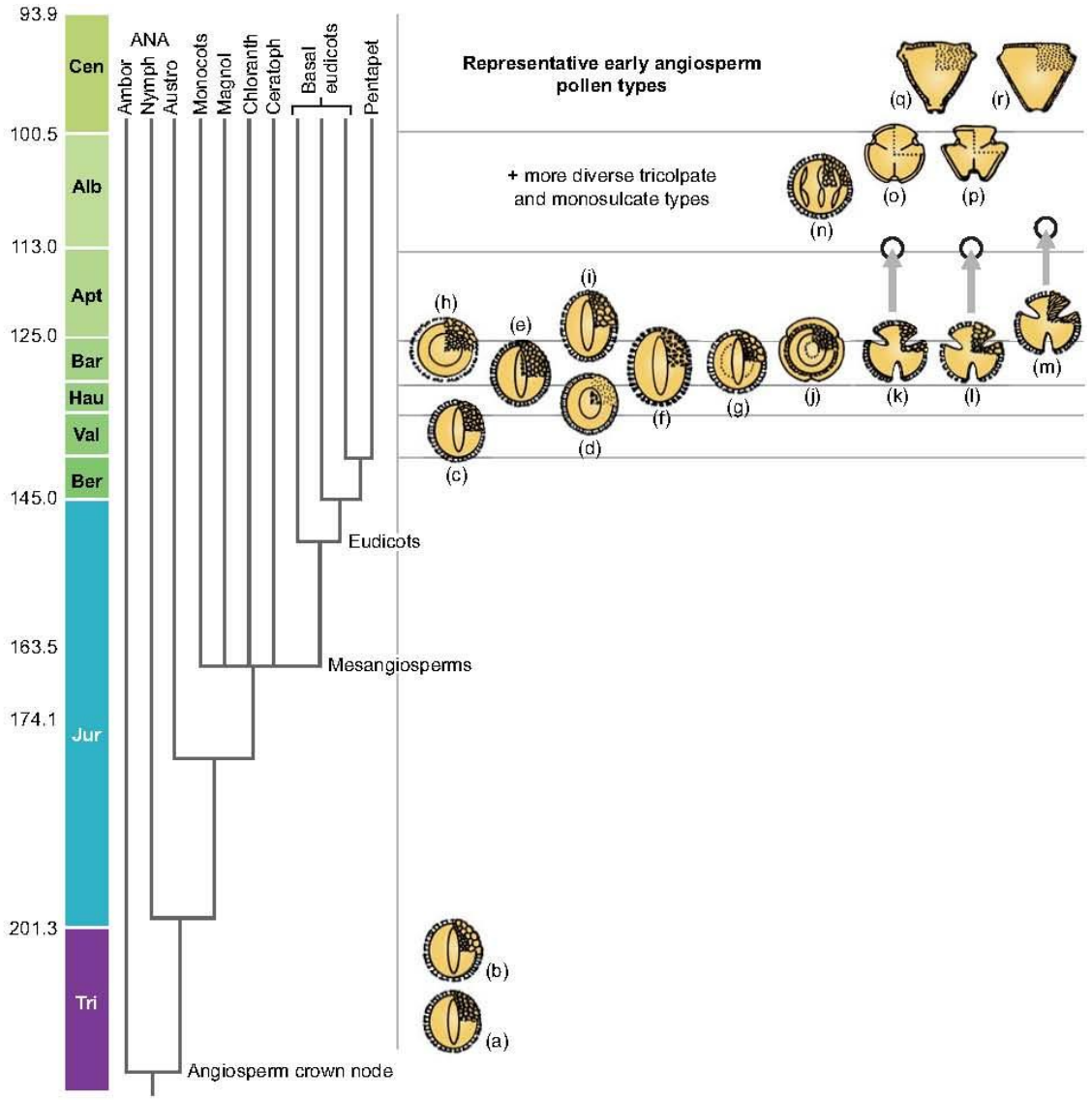

Figure 1

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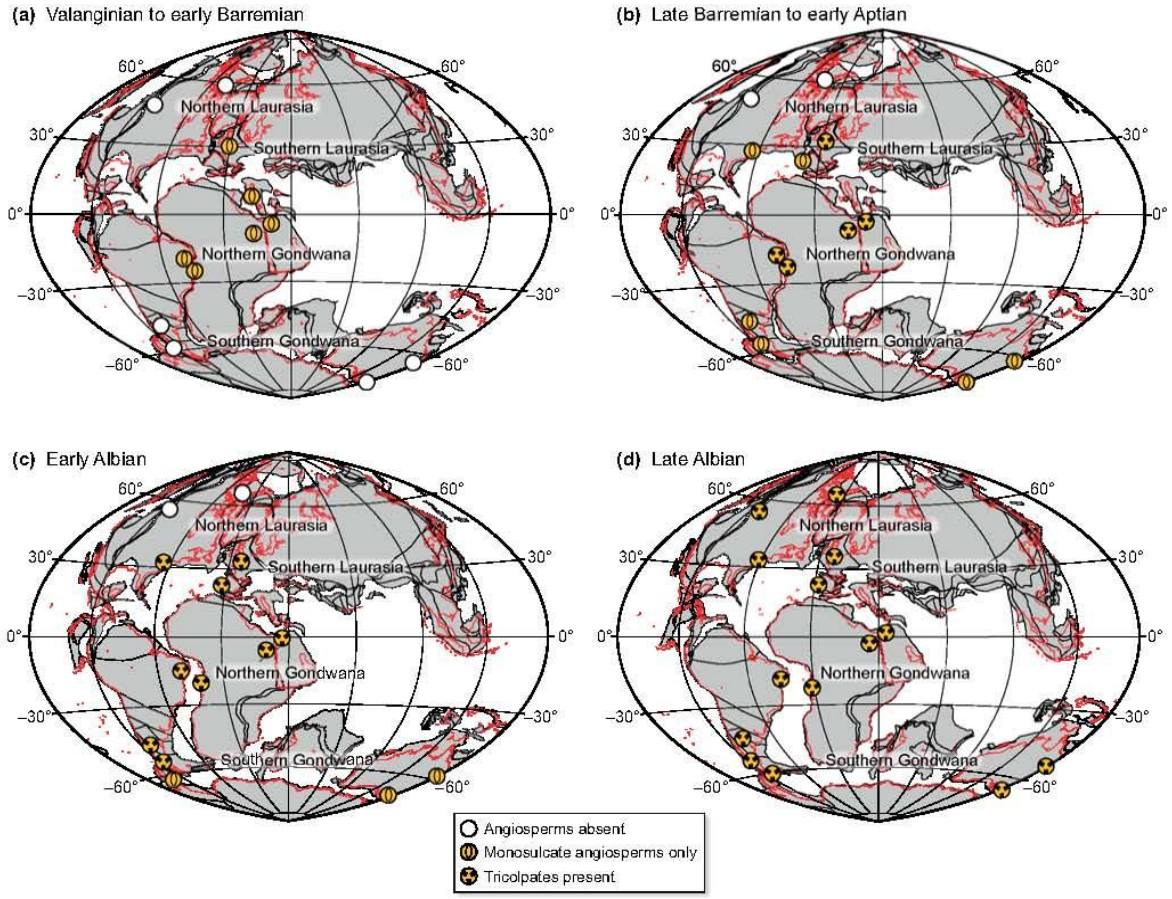

Figure 2

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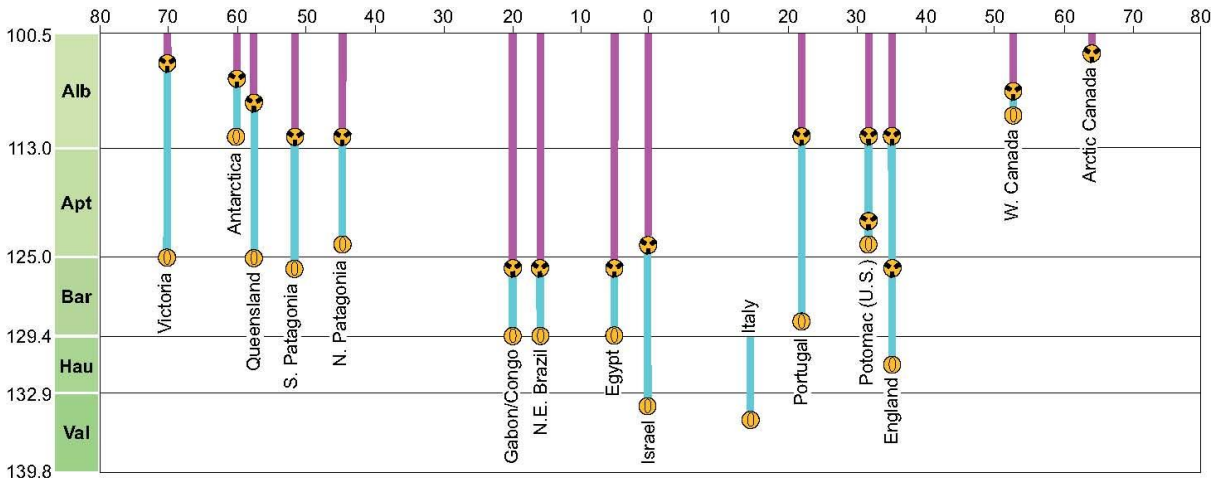

Figure 3

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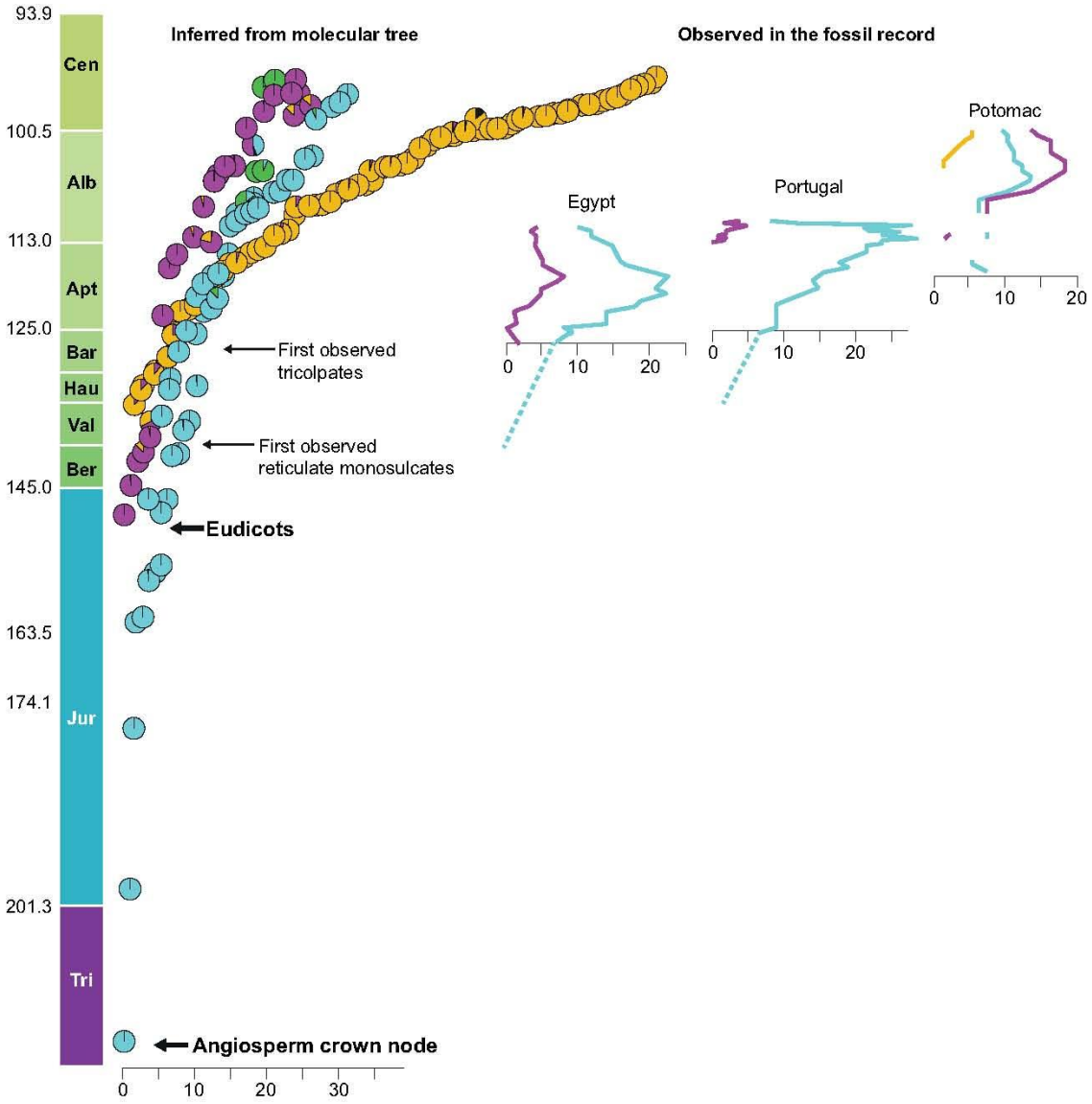

Figure 4

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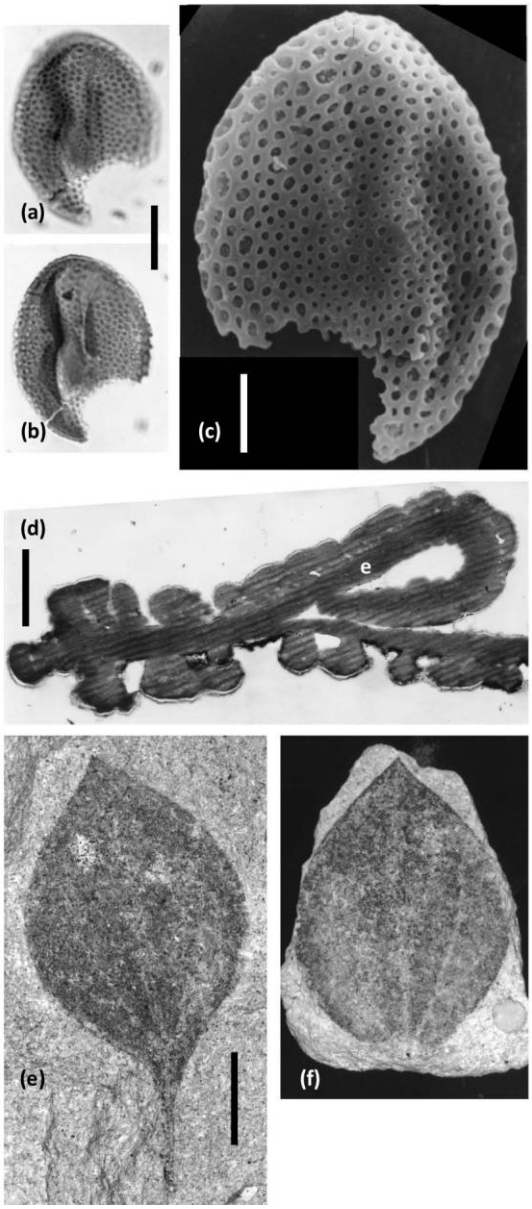

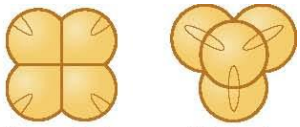

Monosulcate tetrad

Tricolpate tetrad

Box 1